

Table 2. Results of stepwise regression analyses describing three measures of orchid resource stores (number of pseudobulbs in a plant, mean volume of pseudobulbs in a plant, and proportion of sheathed pseudobulbs in a plant) as a function of up to four environmental variables (soil depth, percent canopy cover, presence or absence of other plants, presence or absence of litter); p to enter/remove = 0.10. Only final models are shown.

| | F | P | r ² |
|---|------|-------|----------------|
| Y = Number of Pseudobulbs | | | |
| X = Soil Depth | 4.88 | 0.037 | 0.18 |
| Y = 7.68 + 1.62 X | | | |
| Y = Mean Volume of Pseudobulbs (cm ³) | | | |
| X = Presence of Litter (0 or 1) | 6.27 | 0.020 | 0.21 |
| Y = 334.66 - 85.22 X | | | |
| Y = Sheathed Pseudobulbs : Total Pseudobulbs | | | |
| X = Presence of Litter (0 or 1) | 4.98 | 0.035 | 0.17 |
| Y = 0.55 - 0.09 X | | | |

The proportion of sheathed pseudobulbs in a plant, our third measure of resource stores, was negatively related to the presence of litter. This runs counter to the apparently beneficial effects of litter as indicated by increases in mean pseudobulb volume. Because the rate at which an orchid plant uses the stored water and nutrients within a pseudobulb is unknown, it is possible that conditions early in the dry season necessitate faster use of stored resources. The proportion of sheathed pseudobulbs at this time of year may indicate current resource demands of the plant and not, as we initially guessed, resource stores that influence survival during the dry

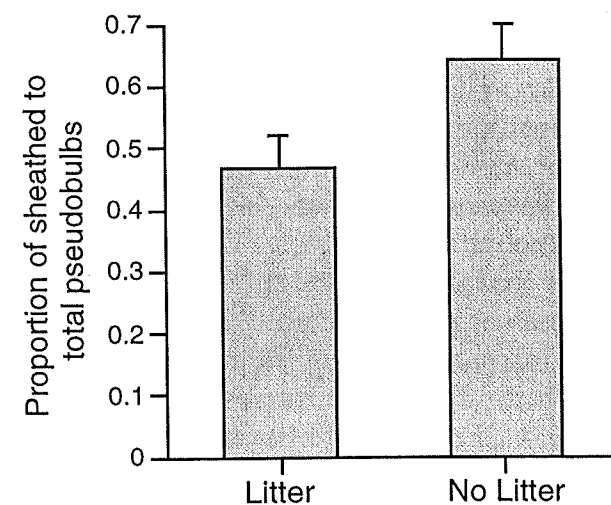


Figure 3. Mean proportion within plants (\pm SE) of sheathed to total pseudobulbs in the presence and absence of leaf litter.

season.

This preliminary investigation of the ground dwelling orchid, *C. paniculatum*, revealed that soil depth and the presence of litter are related to resource stores as measured by number and mean volume of pseudobulbs in a plant. Microhabitat conditions may therefore influence orchid fitness within this population. Additionally, our study supports the use of pseudobulbs morphology as a surrogate of plant fitness when resources are patchily distributed.

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RESPONSES OF *NEPTUNIA PLENA* TO POTENTIALLY HARMFUL AND HARMLESS STIMULI

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Abstract: *Neptunia plena* (Fabaceae: Mimosideae) is an aquatic plant that reacts to physical stimuli by folding its sub-leaflets in towards its central vein. Because this defense is energetically costly, we hypothesized that *N. plena* is able to differentiate between stimuli, and will respond more to those that are potentially harmful. We predicted that *N. plena* would defend itself less against a wind stimulus, which is harmless, than a tactile stimulus, which could indicate herbivory. We tested this by comparing leaflet widths after 1 and 10 disturbances, and then calculating the percent recovery of the leaflet. Plants recovered more quickly from wind disturbance than from tactile disturbance. Plants habituated to the harmless wind stimuli, whereas plants sensitized to the potentially harmful tactile stimuli. Thus, plants distinguish among stimuli, and may be maximizing photosynthesis while minimizing damage from herbivores. Future research might explore whether or not there are disturbance thresholds in plants that utilize nastic movements.

Key Words: marsh, nastic, sensitive mimosa

INTRODUCTION

Neptunia plena (Fabaceae: Mimosideae), an aquatic plant of tropical marshes, responds to physical stimuli by folding its sub-leaflets in towards its central vein. This nastic movement may prevent desiccation in very strong winds and/or disrupt insect herbivory (Raven et al. 1986, Mooney et al. 1998). This defense involves a collapse of the sub-leaflets due to a rapid change in turgor pressure in motor cells at the base of the sub-petiole (Curtis and Barnes 1989). This response may be beneficial but is energetically costly. Most of the energy in the response process is expended as the plant reopens its leaflets (Mooney et al. 1998). There are also photosynthetic costs from the decreased capture of sunlight. Because the leaflet response to stimuli is energetically expensive, it would be beneficial for *N. plena* to distinguish potentially harmful stimuli from harmless stimuli.

The marsh environment where we found *N. plena* is often windy and has many herbivorous insects. Although strong winds may desiccate *N. plena*, it would seem maladaptive for leaflets to close in response to weak winds. In contrast, insects may cause

damage to the leaflets through herbivory so in this case the benefits of closing leaflets may outweigh the costs. Thus, it should be adaptive for *N. plena* were able to distinguish between a wind stimulus and a tactile stimulus (caused by an herbivore). We hypothesized that *N. plena* is able to differentiate between stimuli, and will respond more to those stimuli that are potentially harmful (e.g., wind vs. tactile). We therefore predicted that *N. plena* would respond less against a wind stimulus than a tactile stimulus.

METHODS

This study was conducted on 14 January 2000 along the edge of the Palo Verde marsh, about 0.5 km SW of the OTS station, Palo Verde National Park, Costa Rica. We selected 10 plants within a 10 m² area, and randomly selected one leaflet per plant for experimental observation. Leaflets were protected from wind by a wind block (1 x 1 m plastic sheet suspended on aluminum poles, placed on the windward side of experimental plants), but still received sunlight.

Each leaflet received two disturbance treatments, one at 10:00, and the second at

approximately 13:00. Five of the leaflets received the tactile treatment in the morning and the wind in the afternoon and the other five received the treatments in the reverse order. During the afternoon the leaflets did not appear to be affected by the previous treatments. Tactile disturbances were created by briefly touching the central vein of the leaflet with a finger, and wind disturbances were created by one of us blowing directly on the leaflet from a distance of 10 - 20 cm. For each treatment, each leaflet received 10 disturbances at 4 min intervals. *N. plena* response was quantified by measuring the initial width of the leaflet, the width 4 min after the first stimulation, and the width 4 min after the 10th stimulation. Initial response = $(W_0 - W_1)/W_0 * 100$, and final response = $(W_0 - W_{10})/W_0 * 100$, where W_0 is the resting state width, W_1 is the width following the initial disturbance, and W_{10} is the width following the tenth disturbance. We calculated cumulative response by subtracting initial response from final response. A negative difference indicated that the leaflet closed less after the 10th disturbance than it had after the first; i.e., it was becoming habituated and responding less to the stimulus. A positive difference indicated that the leaflet was closing more after the 10th disturbance (i.e., it was becoming sensitized and increasing its response). We then compared the responses to wind vs. tactile disturbance using a paired t-test.

RESULTS

The percent difference in leaflet width for the tactile disturbance was positive (mean \pm SE = $25\% \pm 7.3\%$, Figure 1). Thus, the leaflets were becoming sensitized and closing more after 10 disturbances than after the initial disturbance. In contrast, leaflets became habituated to wind disturbance (cumulative response = $-10 \pm 4.1\%$, Figure 1). The difference in leaf response to wind vs. tactile stimu-

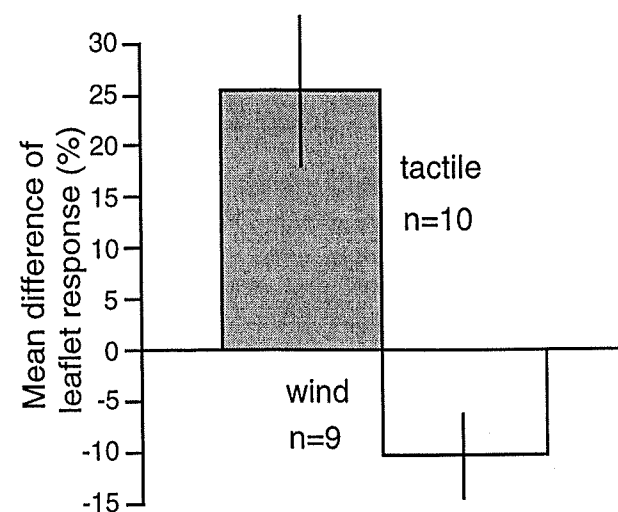


Figure 1: Mean percent difference in width between initial and final disturbances of *N. plena* leaflets in response to tactile and wind disturbances (means \pm 1 SE). Positive values indicate increasing sensitivity and negative values indicate habituation.

lation was highly significant (paired $t = 4.65$, $df = 8$, $p < 0.001$).

DISCUSSION

Our results supported the hypothesis that *N. plena* differentiates between stimuli, and responds more to stimuli that are potentially harmful. After repeated disturbances, *N. plena* had a reduced response to wind stimuli compared to tactile stimuli. We offer two possible explanations for these differing responses. First, the different responses to the two stimuli may optimize the cost to benefit ratio of responding by maximizing solar exposure and minimizing damage from herbivory and trampling. Such an optimization would include reduced response to harmless disturbances and greater response to harmful disturbances.

Second, there may be a disturbance threshold that separates a strong response from a weak response. In our experiment, *N. plena* may have responded to the intensity rather than the type of disturbance. It would be advantageous for *N. plena* to respond more

to an intense disturbance, such as from an herbivore, than to a weak disturbance, such as that from wind. It has been hypothesized that strong winds may desiccate *N. plena* (Raven et al. 1986). Perhaps a wind that reached the disturbance threshold would incite the same response we observed from tactile disturbance.

The ability to respond differently to different kinds of disturbances should be useful in habitats with varying intensities of disturbance, which correlate to varying degrees of threat. A plant that can discriminate between harmful and harmless stimuli should be selected over plants that can not. Future research might explore whether or not there are disturbance thresholds in plants that utilize nastic movements.

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